AVIAN HABITAT SELECTION IN THE ATTENUATED RIPARIAN FOREST ON THE TALLGRASS PRAIRIE

by

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INTRODUCTION

Avian habitat selection has generally been studied on a large geographical scale. For example, habitat components correlated with the presence or abundance of a particular species have been identified in large areas of contiguous vegetation (e.g. Smith 1977, Rice et al. 1983). Comparisons have been made between the key habitat characteristics in different types of habitat (e.g. MacArthur and MacArthur 1961, Karr and Roth 1971, Willson 1974) and also between one type of habitat in various localities (e.g. Cody 1968, Pearson 1975, Rotenberry and Wiens 1980). Many patterns in ecology have been discovered on this broad geographical scale, but the high amount of variation masks many patterns on a more local scale (Wiens 1981). These small scale dynamics are more important in understanding and predicting community structure and function. The woody riparian areas on the tallgrass prairie present an opportunity for a small scale study of avian habitat selection.

In the Flint Hills region of eastern Kansas, bottomland areas support a well-developed riparian forest while the hilltops and slopes are tallgrass prairie. Projecting up the creeks into the prairie are numerous fingerlike extensions of trees, the attenuated riparian forest. Moving upstream, these extensions become narrower and more shrubby as a result of decreasing amount of water and greater

effects of fire. Thus there is a gradient in the attenuated riparian forest characterized by increasing cover and density of shrubs, decreasing numbers of trees, and decreasing width of the woody canopy perpendicular to the general stream course.

The objective of this study was to identify habitat features that are important in organizing the avian community along the gradient from a well-developed gallery forest to a shrubby thicket with only scattered trees. Another objective was to compare patterns of avian distribution and species richness in the attenuated riparian forest on the tallgrass prairie to the eastern deciduous forest. It was assumed, a priori, that species found in the forested regions in the lower reaches of the streams would be present moving up the gradient until the point where the habitat was no longer suitable. Likewise, birds found in the brushy regions would be present moving down the gradient until the habitat was not suitable.

STUDY AREA & METHODS

Study area

Research was conducted at the Konza Prairie Research Natural Area, a 3487 ha native tallgrass prairie site located in the Flint Hills of Riley and Geary Counties, Kansas, which is owned by the Nature Conservancy and administered by the Division of Biology at Kansas State University. The hilltops and slopes are dominated by big bluestem (Andropogon gerardii), Indian grass (Sorghastrum nutans), and little bluestem (Andropogon scoparius). The creek bottoms support a riparian forest which makes up about 6% of the total area of Konza (Killingbeck 1984). This forest is dominated by bur oak (Quercus macrocarpa), hackberry (Celtis occidentalis), and chinquapin oak (Quercus muehlenbergii). Further upstream in the middle portions of the narrowing wooded riparian zone, sycamore (Platanus occidentalis), American elm (Ulmus americana), and honey locust (Gleditsia triancanthos) become interspersed with the oaks. The plant community at the upper reaches of the streams is dominated by small trees and shrubs such as redbud (Cercis canadensis), rough-leaved dogwood (Cornus drummondii), prickly ash (Zanthoxylum americanum), and American elm (Freeman and Hulbert 1985). At the highest elevation, the streams are bordered by prairie.

Methods

Site selection-A map of Konza was overlain with a network of grids approximately 125m on a side. All grids that contained woody riparian vegetation connected downstream to a riparian forest were separated into three categories based on the amount and type of woody growth. The "thick" category consisted of areas 75+m wide made up mostly of trees. The "medium" category consisted of areas narrower than 75m that were largely trees and wider areas that contained both trees and brush. The "thin" category were the open areas with scattered trees and the areas that were highly shrub dominated with only a few trees. All sites were placed into these categories; and thirty sites, ten in each category, were randomly selected for further study using a random number chart.

The width of the woody vegetation >1m in height was measured perpendicular to the general course of the stream for each of the sites in the medium category to determine the median width of woody vegetation for all sites. The median width for this medium category was 69.5m and was used to define the critical area within the 125x125m grids selected for study in order to standardize the area for territory mapping between the three categories. With the aid of a map of Konza Prairie (1:20,800) and aerial photos (1:2500), the center point of all grids was located and

flagged. A circle was laid out with several flags whose diameter was the median width described above.

Territory mapping-Territories were mapped for all birds whose territory included part of this circle. Territory mapping took place between 0600 and about 0930 on at least two, and often three mornings per site, with the first of the three being in the late morning (e.g. 0930-1130). Birds of prey and vagrant species were ignored. Birds that were not territorial or had a home range rather that a territory were not studied. Some of these excluded species were the red-headed, red-bellied, downy, and hairy woodpecker, northern flicker, blue jay, American goldfinch, yellow-billed cuckoo, American robin, and common grackle. For the species of interest, individual singing males were followed and their locations noted on a map of the area to delineate the extent of their territory. The boundaries of the territories were drawn on the map and the center point was determined for habitat sampling.

Habitat sampling-A line 40m long with a random compass orientation passing through the center point of the territory was set up for habitat sampling. A stop was made every 2m along the line at which point litter depth, ground vegetative, shrub, and canopy cover were determined. Ground vegetative cover was that which was <1m tall and was classified as grass, forb, or shrub. Shrub canopy was defined as >1m and <3m tall. Canopy cover was >3m tall.

Shrub and canopy cover were measured with the aid of an ocular scope, modified from James and Shugart (1970). Looking at the angled mirror on the bottom of the tube enable you to sight up the tube through the crosshairs at the top while the tube was held vertically in front of the body. A hit or a miss was recorded at each stop for all of the cover variables. The total number of hits divided by 20 times 100 gave a percent cover value. These values were arcsine transformed prior to statistical analysis. If the territory was less than 40m wide, stops were made at 1m intervals until a sample size of 20 was obtained.

Woody stems were counted in the center .01 ha of the territory (circle with a radius of 5.6m) and classified as to species. Using a Baltimore "reach stick" (Forbes 1955), they were placed into the following size classes based on their diameter breast high: <2.5cm, 2.5-9.9cm, 10.0-30.0cm and >30cm. Dead stems of all species were lumped together and also placed into the above size classes.

Canopy height was determined using a triangulation device at 4 separate points 5m from the center of the territory. The height values from the four points were averaged. The width of the woody vegetation perpendicular to the general course of the stream was determined from the center of each territory. The canopy width was separated into three categories: tree (3m or higher), brush (1-3m

high), or open (less than 1m), only taking note of the highest canopy present. Three variables were constructed from these values. The tree canopy width divided by the total canopy width (i.e. tree + brush + open) described the importance of trees in the overall woody canopy. Similar variables were constructed for the brush and open areas.

The above protocol was followed for each bird's territory that was within the median width circle (diameter-69.5m) at a particular site. On two occasions territories were included where the observed territory edge seemed to be within 10m of the circle. It was assumed that the territory probably was within the circle but was not noted given the brief observation period. When sites were adjacent (i.e. only 125m apart), territories were mapped simultaneously for both sites, but more than two days were spent there. If a territory overlapped two adjacent sites that were being mapped simultaneously, the measurements from that territory were only used once in the statistical analysis. To avoid confounding time effects with categories, sites were studied alternately from each category (e.g. thin, medium, thick, thin, medium, thick, etc.).

Block et al. (1987) found that visual estimation of habitat characteristics by different observers yielded significant differences between estimated values and the actual measured values for many of the habitat variables tested. This suggests a tradeoff between the time savings

with visual estimation and the higher accuracy in actual measurements. All habitat variables in this study were actual measurements (e.g. size class of woody stems) or combinations of measurements and estimates (e.g. percent cover values). The bias in these techniques is assumed to be less than that in visual estimation procedures. All habitat measurements were obtained by the author, so no inter-observer variation was introduced. Measurements that were biased would be consistently biased for all territories.

Statistical Methods

Principal component analysis (PCA) is a multivariate statistical tool that is useful is understanding data sets with many variables. PCA constructs linear combinations of the variables (principal components), each of which explains the maximum amount of the remaining variation possible and are orthogonal to all preceding principal components. Thus there is a reduction of the number of variables to be considered while retaining most of the variation in the data set.

Preliminary analysis of variance of each of the 22 original habitat variables yielded 15 that showed significant differences between species. Using the SAS computer program, principal components analysis was performed on these 15 habitat variables from 113 territories

of the eleven species being studied. The correlation matrix was used in the analysis, which has the same effect as standardizing all the variables. Pearson product moment correlations were calculated between principal component scores and values for habitat variables to test whether a habitat variable had a significant effect in determining the principal component axis (i.e. test the significance of the loading factors of each principal component). PCA assigns values for all principal components for each bird's territory. Analysis of variance was performed on the actual scores for both principal components to detect any significant differences between species along the axis represented by each principal component.

Mean values for PC1 and PC2 were plotted and confidence ellipses calculated after the method of Sokal and Rohlf (1969). A constant was added to the principal component scores to eliminate all negative values prior to these calculations. Seventy-five percent confidence ellipses were calculated rather than 95% confidence ellipses in order to show differences between species more clearly. Interpreting such ellipses is similar to interpreting confidence limits in the univariate case; if many samples were drawn from the population and many such confidence ellipses calculated, (1-a)% of them would contain the true mean. In order to remove the bias introduced by unequal sample sizes, PC scores from

5 randomly selected territories for each species were chosen (5 being the sample size for the brown thrasher, northern oriole, and rufous-sided towhee) Seventy-five percent confidence ellipses were calculated for all species on the basis of these individuals.

Pearson product moment correlations were also calculated between PC1 and PC2 scores for each species individually. While the principal component axes are orthogonal, scores for an individual species may not be, as might be indicated by a slanted confidence ellipse.

RESULTS

Of the more than 40 species that were observed during the summer of 1987, there was a total of 22 species which had at least 1 territory mapped (Table 1). These species and their scientific names are listed in Appendix 1. For 11 of these species, less than 5 individual territories were mapped, so they were not included in any type of statistical analysis. The 11 remaining species are the basis of the statistical analysis presented below.

Preliminary analysis of variance showed significant differences between species for 15 of the 22 habitat variables that were measured (Table 2). Because the 7 nonsignificant variables did not add any relevant information, they were dropped from further analysis.

Principal component analysis-The first two principal components from PCA explained 59% of the total variation (Table 3). Successive principal components explained only small amounts of variation and were not considered on the basis of the scree principle (Pielou 1984). Principal component 1 (PC1), which explained 40% of the total variation, had "high" negative loadings for variables associated with brush and "high" positive loadings for variables associated with forested areas. Thus, PC1 describes a gradient from brushy areas with many small woody

stems to forested areas with a high closed canopy of large trees. Pearson product moment correlations between PC1 scores and habitat variables were the basis of interpretation for the loading factors (Table 4). Analysis of variance for the actual PC1 scores showed significant differences between species which can be summarized in the following lines diagram, in which species underlined with a common line are not significantly different:

WBN EWP TTM NOR HWN BCC CAR GCF BTH RST FSP

Principal component 2, which explained 19% of the variation, had "high" negative loading factors for variables associated with grassy, open areas and "high" positive loadings for habitat variables associated with the brushy thickets. Thus, PC2 describes the interplay in the upper reachs of the streams between open areas with only scattered woody riparian vegetation and areas that are entirely brushy. Table 5 contains the Pearson product moment correlations between PC2 scores and the 15 habitat variables used in the analysis. Analysis of variance of the PC scores showed that there was broad overlap between the species but that the field sparrow was significantly different than all other species.

Figure 1 shows a plot of PC2 on PC1 with only the mean responses for each species shown. The eleven species fall out into three groups on the basis of this plot. One group

of birds, made up of the tufted titmouse, eastern wood-pewee, white-breasted nuthatch, and northern oriole, are only found at high values of PC1 or in the forested areas. Another group, made of the field sparrow, brown thrasher, and rufous-sided towhee, select those areas with low values of PC1 or the brushy thickets at the upper reaches of the streams. This group is further separated by PC2 with the field sparrow selecting the grassy open areas and the brown thrasher and rufous-sided towhee found in the brushy areas. The mean responses of the last group, consisting of the northern cardinal, black-capped chickadee, great crested flycatcher, and house wren, are at intermediate values of PC1, but they are actually found throughout the forest to brush gradient described by PC1.

In Figure 2, confidence ellipses for each species' mean response are plotted. On the basis of the principal components, there is considerable overlap in the characteristics of the habitat selected within each of the groups outlined above. Between groups there is minimal overlap, indicating that overall the groups are selecting different types of habitat and that any overlap is occurring at the tails of the distribution of each species. Pearson product moment correlations between PC1 and PC2 for each species were not significant at a=.05 for any species indicating a lack of correlation even though some ellipses in Figure 2 are slanted.

Because the size of the confidence ellipse is very sensitive to the sample size, Figures 3, 4, & 5 present confidence ellipses calculated from 5 randomly selected individuals of each species in the forest, brush, and generalist groups, respectively. The combined ellipses are shown in Figure 6. The generalist group has the largest confidence ellipses because they are found throughout the gradient described by PC1. The forest and brush birds have relatively smaller ellipses, indicating they are more restricted in their habitat selection along the forest-brush gradient.

DISCUSSION

Experimental design considerations

The woody riparian vegetation contained light gaps in the forested regions, dead snags, brushy undergrowth, open grassy areas, and dogwood thickets, all of which contributed to the patchiness of the vegetation. The patchiness was on a smaller scale than that of a bird's territory so that a single territory covered several to many different patches. Measurements of habitat variables may or may not have overlapped one or more types of patches, leading to higher variance in the habitat variables for all species. Due to time constraints, the mapping techniques employed gave a general rather than precise territory boundary, yet the measurements taken for a particular bird were definitely within the area used by the bird, whether or not it was the very center of its territory. These habitat sampling and mapping techniques, coupled with a patchy habitat, resulted in measurements with high variability indicating large amounts of overlap in habitat use. More careful mapping techniques and habitat sampling designed to account for the patchiness that is present would no doubt show more subtle differences in habitat selection between the species.

There were no particular species selected for study prior to commencing fieldwork. This led to time being spent mapping territories and measuring vegetation for species

which were not included in later analysis because of small sample size. Sample sizes for the eleven species in this study are not very statistically robust, but they force interpretations to be conservative. More confidence can be placed in any differences that are detected because errors would be made in the direction of failing to detect marginally significant differences. The selection of five random individuals from each species for the confidence ellipses in Figures 3-6 resulted in a loss of information for most of the species. However, this process does eliminate the problem of different size ellipses caused by unequal sample sizes, and it does illustrate differences in habitat selection between species more clearly.

Comparison with the eastern deciduous forest

The woody growth in the riparian areas on the tallgrass prairie forms a transitional zone between the forest and the tallgrass prairie, or an edge. The higher avian density often found in these ecotonal regions is termed the edge effect and is partially due to species from both the forest and prairie habitats occurring together, plus the presence of species unique to the ecotonal zone (Gates and Gysel 1978). Edge habitat has greater relative importance in small wooded areas than in extensive forests. These small forest tracts have a high density of edge species, which preclude any forest-interior species (Ambuel & Temple 1983).

The number of bird species is positively correlated with the size of a forested area (Galli et al. 1976, Martin 1981). In a study of forest remnants near Ottawa, Canada, Freemark and Merriam (1986) found that the size of the area is particularly important for the forest interior birds, many of which are long-distance migrants. Habitat heterogeneity, on the other hand, seems to be more important than area for edge species. The forested areas on the tallgrass prairie are only narrow riparian strips ranging from about 50 to a maximum of 2-300 meters wide in the meandering lower reaches of the streams. The attenuated riparian forest in the upper reaches of the streams contains a higher proportion of brushy growth and is even less suitable to species with areal constraints but more suitable to species requiring habitat heterogeneity. Species which have area limitations are not likely to be abundant in the woody riparian vegetation on the tallgrass prairie, although some species may be present in very low numbers (see below).

Askins and Philbrick (1987) also point to the importance of the size of the regional forest. When surrounding forest areas were cut during 1953-1976, there were lower numbers of long-distance migrants present at their 23 ha study site; abundances then increased after 1976 due to reforestation in the region. While Askins and Philbrick did not note a critical size below which long-

distance migrants would eventually be eliminated, Wilcove (1985) measured relative predation rates by placing artificial nests containing quail eggs in various sizes of forest tracts and found higher rates in smaller forest tracts. Even in "large" forests of up to 900 ha, the relative predation rates were still higher (18%) than those in a "pristine" forest of 209,000 ha (2%). He suggests that long-distance migrant songbirds that build open nests near the ground could disappear from all but the largest forest tracts due to higher predation rates in the smaller forests.

In the eastern deciduous forest in Maryland, Whitcomb et al. (1981) found a species pool of 73 species available for colonization of small forest tracts after eliminating raptors, birds associated with water, upland game birds, and nocturnal birds (Table 6). Of the species found on Konza Prairie (Zimmerman 1985), 49 are summer residents in the woody riparian vegetation on Konza Prairie, using the same qualifications as above (Table 6). Comparing the species lists from the two areas, the forest interior neotropical migrants are the group that is most lacking in the riparian woodland species pool of the tallgrass prairie. This is to be expected given the size dependence (Freemark and Merriam 1986) and the importance of the regional forest (Askins and Philbrick 1987) to these forest interior, long-distance migrants. Both of these important factors are lacking in the riparian forest on the tallgrass prairie. This group is

probably not as well represented as the number of species alone might indicate. Approximately equal proportions of the other groups from the eastern deciduous forest in Maryland are present in the riparian woody vegetation on the tallgrass prairie (Table 6). Several of the forest interior, neotropical migrants that are found in the riparian forest on the tallgrass prairie are present only in low numbers, including the Kentucky warbler, scarlet tanager, summer tanager, and rose-breasted grosbeak. Although no direct evidence has been obtained, they probably do breed on Konza Prairie. In comparison with large areas of the eastern deciduous forest, Wilcove (1985) listed the following species as characteristically absent from most or all small woodlots in Maryland and Tennesee: veery, yellow-throated vireo, northern parula, black-and-white warbler, ovenbird, Kentucky warbler, hooded warbler, and the scarlet tanager.

Whitcomb et al. (1981) also calculated a tolerance to fragmentation for species in the eastern deciduous forest in Maryland by dividing the number of territories/point survey in forest islands 6-14 ha by the number in forests 70 ha or larger. If this ratio was equal to or greater than one for a species, this species had no size limitations and was distributed independently of the size of the forest tract. If the ratio was less than one, then the species had some

type of areal constraints and would be found primarily in larger forests. Most of the species known to breed in the riparian areas on Konza Prairie which were included in Whitcomb's study (exceptions include the tufted titmouse=.87, the mourning dove=.89, blue-gray gnatcatcher=0.0, and yellow-billed cuckoo=.14) had a value greater than or equal to one, meaning these species were not constrained by the size of the forest. This high tolerance to fragmentation is obviously a prerequisite for birds that are found in the woody riparian vegetation on the tallgrass prairie because of its small area and its narrow width which maximizes edge habitat and minimizes any forest interior habitat. Most of the species in Whitcomb's list which are not summer residents in the woody riparian areas on the tallgrass prairie have a tolerance to fragmentation less than 1 (exceptions are the Carolina chickadee and the Carolina wren, which are replaced geographically by the black-capped chickadee and the house wren, respectively). Because of similar avifaunas, except for those species with area limitations, the riparian forest on the tallgrass prairie can still be considered a part of the eastern deciduous forest, although a rather small and far-flung portion of it. Lower avian diversity in the riparian forest on the tallgrass prairie is primarily due to the small areas of the forest segments, which eliminates forest interior species, and the lack of a regional forest, which

would have more species available for colonization.

Selection of habitat

The basis of the separation of the eleven species into three groups was on the type of habitat that each species selected. There are many other niche axes in the n-dimensional hypervolume (Hutchinson 1957) which could be used as a basis of separation. Habitat selection, however, is a good place to start in describing the niche of a bird.

A working definition of habitat selection is the bird's choice of areas that will lead to an increase in its fitness (Rosensweig 1985, Hutto 1985). The birds in this forest-brush gradient are found there rather than somewhere else presumably because of a differential increase in fitness there. One must assume than birds which selected this habitat had a higher fitness than those in other habitats and were more likely to leave offspring in future generations, resulting in the present species distributions.

Studies of habitat selection implicitly assume that the habitat features found to be important are the same or are correlated with the features that are the actual cues for the bird as it selects its habitat. These studies can only establish correlations between habitat variables and the presence of a species; they cannot assume the habitat variable is the causal agent for the species' presence. Even if the proximate cues can be identified, they are not

necessarily the same as the ultimate cause. While a bird may respond to a certain habitat structure (the proximate cue), the important factor from an ultimate standpoint may be the abundance of food, escape from predators, or other factors. Principal components analysis requires no a priori judgments as to the importance of certain variables but evaluates variables on the basis of their ability to explain variation in the data set. As a result, PCA has been widely applied in many habitat selection studies.

Species which are found in a particular type of habitat ideally are distributed independently of each other and are found in the same habitat because they respond in like fashion to habitat structure or other proximate cues. This ideal situation is realized only when the species have no biotic interactions, as Rotenberry and Wiens (1980) suggested to be the case in an analysis of communities in North American steppe vegetation. Competition, which has long been suggested as the dominant force in organizing community interactions (e.g. Cody 1974, MacArthur 1972), would change this ideal distribution of species. In a study of shelterbelts in South Dakota, Martin (1981) found fewer species present in a guild than were possible, given area constraints, which he attributed to competition between members of guilds. In the eastern deciduous forest, Hespenheide (1971) never found more than two flycatcher

species, which divided food resources on the basis of size.

A priori assumptions of equilibrated communities in regard to resource use or competition based on food resources may not be justified (Wiens 1977). Large amounts of overlap in diet has been shown in several groups of birds. Four species of blackbirds in a central Washington pothole had very similar diets although there were some differences in foraging technique (Orians and Horn 1969). Five species of finches wintering in oldfields North Carolina had almost 100% dietary overlap but had some differences in seed size and habitat utilization (Pulliam and Enders 1971). Grassland birds typically show a high degree of multidimensional niche overlap (Rotenberry and Wiens 1980). Events on the wintering range are probably the limiting factor for many species, not food resouces on the breeding range (Fretwell 1972). Avian communities that experience a predictable overabundant resource peak are an extreme example of non-equilibrium conditions. Rosenberg et al. (1982) found 8 of 12 insectivorus bird species in a riparian area in Arizona heavily utilized (30-80% of diet) emerging annual cicadas in their diet. In all 8 species, the time of fledging young coincided with peak cicada numbers, which were up to ten times greater than the total metabolic demand of the bird community. While most communities face somewhat limited resources, careful studies are needed to determine the role of competition in that

community.

Habitat characteristics

Forest-Habitat that was selected by the species in this study was similar to that reported in the literature as being characteristic for the species. The eastern wood-pewee is found in upland hardwood study areas in Missouri (Kahl et al. 1985). Other characteristics reported as important are a few small trees and many large trees (Robbins 1978) with high canopy closure (Weber and Theberge 1977). Connor and Adkisson (1975) found mature oak stands with canopy heights >8m were suitable for the tufted titmouse. Some subcanopy development seems to be important (Evans and Kirkman 1981), and snags with secondary cavities for nesting must be available (Evans and Conner 1979). The white-breasted nuthatch is found in pole to mature forests in Missouri (Kaht et al. 1985) with large trees (DeGraaf et al. 1980) with high canopy closure (Anderson 1979). The habitat of the northern oriole is described by tall trees and a shrub layer for foraging habitat (Sibley and Short 1964). They are found in the riparian forest along the Missouri River (Kahl et al. 1985).

Brush-The field sparrow is found in brushy old fields (Kahl et al. 1985) or grasslands with small trees that are used as song perches (Gates and Gysel 1978). The brown

thrasher selects areas with large numbers of small woody stems and shrubs (Kahl et al. 1985), few trees, and dense ground cover (James 1971). The habitat of the rufous-sided towhee is brushy areas with low canopy height (Nolan 1963, Robbins 1978) and a well developed litter layer (Meanley 1966).

Generalist-Important factors in the habitat of the great crested flycatcher are a well-developed understory (Johnston and Odum 1956), proximity to or presence of mature forest (Kahl et al. 1985), and the availability of cavities for nesting (Evans and Conner 1979). The black-capped chickadee is found primarily in forest edge situations but also in habitats ranging from mature forests to brushy grasslands (Davis and Savidge 1971). In Missouri, the house wren is found in areas with large numbers of small woody stems and lower numbers of larger stems (Kahl et. al. 1985). The northern cardinal requires adequate foliage density in the vicinity of the nest (Dow 1970, Ehrhart and Conner 1986) and are found in a wide variety of habitats (Harrison 1975).

Diet and other niche separations

The species within each of the three groups select habitat with similar vegetative structure. The competitive exclusion principle, which says that species with identical niches cannot co-exist indefinitely (Hardin 1960), would indicate that there must be other differences separating the

niches of each species within a group. These factors include types of food eaten, type and location of foraging, nesting ecology, reproductive strategies, and others represented by different axes in the n-dimensional hypervolume of the niche (Hutchinson 1957).

Forest-Within the forest group, the eastern wood-pewee is the only flycatcher. McAtee (1926 cited in Bent 1942) found that its diet consisted of dipterans (30%) and hymenopterans (28%) with smaller amounts of coleopterans (14%) and lepidopterans (12%). The white-breasted nuthatch forages for coleopterans, arachnids, caterpillars, and various types of larva (McAtee 1926 cited in Bent 1948) along the bark of trunks and large branches (pers. obs.). According to Beal et al. (1916 cited in Bent 1946), the tufted titmouse is a canopy gleaner whose diet includes >50% caterpillars plus large numbers of hymenopterans and lesser amounts of coleopterans and fruit. The northern oriole eats caterpillars, various larvae, slow insects, and occasional fruit and nectar (Pleasants 1979). Two of the species (TTM & WBN) nest in old woodpecker cavities or natural cavities in dead snags (Bent 1946 & 1948). The eastern wood-pewee builds an open nest on small twigs, and the northern oriole builds a woven hanging nest at the ends of branches (Bent 1942 & 1958).

Brush-The field sparrow was distinct from the other two members in the brush group based on its habitat selection

alone. Allaire & Fisher (1975) found the field sparrow forages for grass and weed seeds within 1 m of the ground. It also eats coleopterans, orthopterans, and caterpillars (Judd 1901 cited in Bent 1968) and feeds them to its young. The brown thrasher forages for coleopterans, caterpillars, hemipterans, and orthopterans on or near the ground (Beal et. al. 1916 cited in Bent 1948). The rufous-sided towhee forages primarily in the litter on the ground for coleopterans (49%) and lepidopterans (19%) supplemented with ripe fruit and seeds later in the season (Franzblau & Collins 1980). Greenlaw (1978) found them to be opportunistic in food habits, taking defoliating caterpillars from the treetops during an outbreak. All three species nest on or near the ground: field sparrow in thick grass (Bent 1968), brown thrasher in shrubs (Best & Stauffer 1980), and the rufous-sided towhee also in shrubs (Davis 1960).

Generalist-The generalist group overlaps both the forest and the brush birds in niche dimensions associated with the structure of the habitat. The great crested flycatcher's diet consists of lepidopterans (21%), coleopterans (17%) hymenoptera and hemipterans (both 14%) (Beal et al. 1912 cited in Bent 1942) which would be bigger than the prey of the other flycatcher, the eastern wood-pewee (Hespenheide 1971). The house wren eats 98% insects,

which it obtains both from the ground and from the trees. These insects consist of hemipterans (29%), orthopterans (18%), lepidopterans (14%), and coleopterans (14%) (Beal 1897 cited in Bent 1948). The northern cardinal eats many types of seeds, fruit, and various insects (McAtee 1908 cited in Bent 1968). The black-capped chickadee gleans caterpillars, arachnids, and various larvae (Kluyver 1961) from the bark of twigs in the subcanopy (Sturman 1968). The main predator of the black-capped chickadee eggs or nestlings is the house wren (Sturman 1968), which is notorius for evicting other birds from their nests (e.g. Sherman 1925). The cardinal nests in shrubs and trees (Ehrhart & Connor 1986); adequate foilage density may be the only nesting requirement (Dow 1969, 1970) while the habitat in the rest of the territory may vary widely (Ehrhart & Connor 1986).

Birds in the generalist group have adaptations to enable them to survive throughout this gradient while overlapping the forest and brush specialists at the ends of the gradient. Adequate foliage density near the nest site seems to be the critical factor for the cardinal (Ehrhart and Connor 1986). This enables it to be found throughout the forest-brush gradient as long as its requirement for nest sites is met. The great-crested flycatcher is the only neotropical migrant in all three groups which is a cavity nester and so experiences lower relative predation rates

than open-nesting species (Wilcove 1985). This may allow the great-crested flycatcher to survive in the upper portions of the forest-brush gradient where all of the woody habitat is edge and predation is higher than in larger forested areas. The house wren and black-capped chickadee are somewhat generalized in their foraging, which may allow them to adjust their foraging behavior depending on their location in the forest-brush gradient. Both are also cavity nesters and may be found in the upper reaches of the streams because there are many nest sites available in snags (see below).

These differences in diet, foraging ecology, and nesting, which are summarized in Table 7, and other factors may be important in enabling these species to co-exist in the same habitat. If different species are foraging for different types or sizes of food items or looking for them in different places, then the species are not competing for those resources and so could co-exist in the same habitat without competitively excluding one another. MacArthur (1958) found five warbler species with almost complete dietary overlap could co-exist by differences in location of foraging. Bell's vireo and Bewick's wren have very similar diets when co-existing in brushy areas on the tallgrass prairie, but select different types of habitat on both the territory level and nest site level (Farley 1987).

Competition for nest sites may be a factor in limiting densities of certain species. The eleven species in this study include five hole-nesters: the black-capped chickadee, great crested flycatcher, tufted titmouse, white-breasted nuthatch, and house wren. Cavity nesting birds may be limited by the number of dead snags available for nests (Cody 1985). However, Brawn and Balda (1988) found only 3 of 6 cavity nesters showed an increase in density when nest-boxes were placed in the northern Arizona ponderosa pine forests. They suggested that other factors such as territoriality, abundance of food, or substrate for foraging may modulate a given species' response. Konza Prairie has a history of aerial spraying of herbicide which has resulted in high numbers of dead snags in the riparian areas. Limitation of cavities for nests is not a problem now, but with the cessation of spraying in Konza's present research use, it may become one in the future.

Other species accounts

There were eleven species which had less than 5 territories mapped and so were not used in the above analysis. However, general comments about them and their habitat selection are in order and are presented below. The species are roughly classified into forest interior, forest edge, and shrub or field birds. These are groups based upon general impressions by the author and not upon data

obtained. Information concerning the abundance of species on Konza is from Zimmerman (1985).

Forest interior-The scarlet tanager is quite rare on Konza Prairie, and the two individuals which were found were in the largest two areas of forest. These were mature gallery forests with large oak and hackberry trees. The summer tanager is somewhat more common on Konza. The one individual was in an somewhat open oak forest with little understory vegetation. Territories were mapped for two rose-breasted grosbeaks in the lower reaches of the streams. Both overlapped areas of forest and open grassy areas. The Louisiana waterthrush was found only along flowing streams in the forested lower reaches of the streams. Later in the summer when the streams were drying up, Louisiana waterthrushes were no longer present.

Forest edge-Indigo buntings were found in and around clearings in the forested regions of the streams. The clearing was included as part of the territory in all cases. Eastern bluebirds were also found in a similar type of habitat. They were found where there was an abrupt transition from forest to prairie rather than where there was a zone of rough-leaved dogwood or other brush in the middle. This may be because of their use of the trees to perch on while watching for insects on the ground. The blue grosbeak was found in the shrubby vegetation in the edge zones and also in the trees nearby. Two blue-gray

gnatcatchers were found; one was in an open forest, and the other was in a brushy area surrounding a clump of American elm trees.

Shrub or field-Bewick's wrens were found in the upper reaches of the streams in areas characterized by a few clumps of trees, grassy open areas, and lots of brush. Bell's vireo was found in dogwood and other brushy patches in the very upper reaches of the streams. The common yellowthroat, which incidentially was one of the author's favorite birds of the summer, was found at the edges of brushy patches of dogwood. One of the territories included a seep and another was along a stream very close to a spring.

CONCLUSIONS

1. Patchiness of the vegetation and sampling techniques led to high variance in the habitat variables. Better techniques could have reduced, but not eliminated, this variance.

2. The riparian forest on the tallgrass prairie has lower avian species diversity because of the small area of the forest which preempts forest interior species and the lack of a regional forest which would contain a larger species pool for colonization.

3. The species that are found in the woody riparian vegetation on the tallgrass prairie are generally the normal avifauna of the eastern deciduous forest except for those species with area constraints.

4. This study, as well as other habitat selection studies, can only correlate habitat features with the presence of a particular species.

5. Competition may be an important structuring force in communities, but this should not be assumed to be the case.

6. The eleven common species in the woody riparian vegetation on the tallgrass prairie fall into three groups with respect to their habitat selection: forest birds are found in the lower reaches of the streams in the areas made up primarily of trees, brush birds are found in the upper

reaches of the streams where there are many shrubs and only scattered trees, and generalists are found throughout the gradient from the forested areas to the brushy areas.

7. The type of habitat each species selected was generally similar to that reported for that species in the literature.

8. Even though the habitat selected by each species within a group is similar, the literature reports other aspects of their niches which separate the species, such as their diet, nesting and foraging patterns.

LITERATURE CITED

Allaire, P. N., & C. D. Fisher. 1975. Feeding ecology of three resident sympatric sparrows in eatern Texas. Auk 92:260-269.

Ambuel, B., & S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Anderson, S. H. 1979. Habitat assessment for breeding bird populations. Trans. North Am. Wildl. Nat. Resour. Conf. 44:431-445.

Askins, R. A., & M. J. Philbrick. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. Wilson Bull. 99:7-21.

Beal, F. E. 1897. Some common birds in their relation to agriculture. U. S. Dept. Agr. Farmers' Bull. 54.

-----. 1912. Food of our more important flycatchers. U.S. Dept Agr. Biol. Surv. Bull. 44.

Beal, F. E., W. L. McAtee, & E. R. Kalmbach. 1916. Common birds of southeastern United States in relation to agriculture. Farmers' Bull. 755.

Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

-----. 1946. Life histories of North American jays, crows, and titmice, Part II. U.S. Natl. Mus. Bull. 191.

-----. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull 195.

-----. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

-----. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies, Parts I & II. U.S. Natl. Mus. Bull. 237.

Best, L. B., D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. Condor 82:149-158.

Block, W. M., K A. With, & M. L. Morrison. 1987. On measuring bird habitat: influence of observer variablility and sample size. Condor 89:241-251.

Brawn, J. D., & R. P. Balda. 1988. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? Condor 90:61-71.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102:107-147.

-----. 1974. Competition and the structure of bird communities. Princeton Univ. Press. Princeton, NJ.

-----. 1985. An introduction to habitat selection in birds. Pgs 3-56 in Habitat selection in birds. (M. L. Cody, ed.) Academic Press, Orlando, FL.

Conner, R. N., & C. S. Adkisson. 1975. Effects of clearcutting on the diversity of breeding birds. J. Forestry 73:781-785.

Davis, D. E., & I. R. Savidge. 1971. Distribution of certain birds in various types of vegetation. Bird-Banding 42:264-268.

Davis, J. 1960. Nesting behavior of the rufous-sided towhee in coastal California. Condor 62:434-456.

DeGraaf, R. M., G. M. Witman, J. W. Lanier, B. J. Hill, & J. M. Keniston. 1980. Forest habitat for birds of the northeast. Northeast. For. Exp. Sta. Eastern Reg. U.S. Dept. Agr., For. Serv.

Dow, D. D. 1969. Habitat utilization by cardinals in central and peripheral breeding populations. Can. J. Zool. 47:409-417.

-----. 1970. Distribution and dispersal of the cardinal (Richmondena cardinalis) in relation to vegetational cover and river systems. Am. Mid. Nat. 84:198-207.

Ehrhart, R. L., & R. N. Conner. 1986. Habitat selection by the northern cardinal in three eatern Texas forest stands. SW Nat. 31:191-199.

Evans, K. E. & R. A. Kirkman. 1981. Guide to bird habitats of the Ozark Plateau. U.S. Dept. Agr., For. Serv. Gen. Tech. Rep. NC-68.

Farley, G. H. 1987. Comparative breeding strategies of two coexisting passerines: Bell's vireo (Vireo bellii) and Bewick's wren (Thryomanes bewickii). MS thesis. Kansas State University.

Forbes, R. D. ed. 1955. Forestry handbook. The Ronald Press Co., New York.

Franzblau, M. A., & J. P. Collins. 1980. Test of a hypothesis of territory regulation in an insectivorous bird by experimentally increasing prey abundance. Oecologia 46:164-170.

Freeman, C. C., & L. C. Hulbert. 1985. An anotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. Trans. Kan. Acad. Science. 88:84-115.

Freemark, K. E., & H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Cons. 36:115-141.

Fretwell, F. D. 1972. Populations in a seasonal environment. Prnceton Univ. Press. Princeton, NJ.

Galli, A. E., C. F. Leck, & R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-364.

Gates, J. E., & L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Greenlaw, J. S. 1978. The relation of breeding schedule and clutch size to food supply in the rufous-sided towhee. Condor 80:24-33.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292-1297.

Harrison, H. H. 1975. A field guide to birds' nests. Houghton Mifflin Co., Boston.

Hespenheide, H. A. 1971. Flycatcher habitat selection in the eastern deciduous forest. Auk 88:61-74.

Hutchinson, G. E. 1957. Concluding remarks. Cold Springs Harbor Symp. Quant. Biol. 22:415-427.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pgs 455-516 in Habitat selection in birds (M. L. Cody, ed.). Academic Press Orlando, FL

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215-236.

James, F. C., & H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Johnston, D. W., & E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37:50-62.

Judd, S. D. 1901. The relation of sparrows to agriculture. U.S. Dept. Agr. Biol. Surv. Bull. 15.

Kahl, R. B., T. S. Baskett, J. A. Ellis, & J. N. Burroughs. 1985. Characteristics of summer habitats of selected nongame birds in Missouri. Univ. of Missouri-Columbia, Col. of Agr., Agr. Exp. Station Res. Bull. 1056:1-155.

Karr, J. R., & R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423-435.

Killingbeck, K. T. 1984. Nitrogen and phosphorus resorption dynamics of five tree species in a Kansas gallery forest. Am. Nat. 105(945):423-435.

Kluyver, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. Auk 78:532-550.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York.

MacArthur, R. H., & J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

McAtee, W. L. 1926. The relation of birds to woodlots in New York state. Roosevelt Wildlife Bull. 4:1-148.

Martin, T. E. 1981. Limitation in small habitat islands: chance or competition. Auk 98:715-734.

Meanley, B. 1966. Some observatons on habitats of the Swainson's warbler. Living Bird 5:151-165.

Nolan, V. Jr. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44:305-313.

Orians, G. H., & H. S. Horn. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50:930-938.

Ott, L. 1984. An introduction to statistical methods and data analysis, 2nd ed. Duxbury Press, Boston.

Pearson, D. L. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. Condor 77:453-466.

Pielou, E. C. 1984. The interpretation of ecological data. John Wiley & Sons. New York.

Pleasants, B. Y. 1979. Adaptive significance of the variable dispersion pattern of breeding northern orioles. Condor 81:28-34.

Pulliam, H. R., & F. Enders. 1971. The feeding ecology of five sympatric finch species. Ecology 52:557-566.

Rice, J., R. D. Ohmart, & B. W. Anderson. 1983. Turnovers in species composition of avian communities in contiguous riparian habitats. Ecology 64:1444-1455.

Robbins, C. S. 1978. Determining habitat requirements of nongame species. Trans. North Am. Wildl. Nat Resour. Conf. 43:57-68.

Rosenberg, K. V., R. D. Ohmart, & B. W. Anderson. 1982. Community organization of riparian breeding birds: response to an annual resource peak. Auk 99:260-274.

Rosenzweig, M. L. 1985. Some theoretical aspects of habitat selection. Pgs 517-540 in Habitat selection in birds. (M. L. Cody, ed.) Academic Press, Orlando FL.

Rotenberry, J. T., & J. A. WIens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228-1250.

SAS User's Guide: Basics, & Statistics, Version 5 ed. 1985. SAS Institute, Inc. Cary, NC.

Sherman, A. R. 1925. Down with the house wren boxes. Wilson Bull. 37:5-13.

Sibley, C. G., & L. L. Short, Jr. 1964. Hybridization in the orioles of the Great Plans. Condor 66:130-150.

Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810-819.

Sokal, R. R., & F. J. Rohlf. 1969. Biometry. Freeman & Co., San Francisco.

Sturman, W. A. 1968. The foraging ecology of Parus atricapillus and P. rufescens in the breeding season, with comparisons with other species of Parus. Condor 70:309-322.

Weber, W. C., & J. B. Theberge. 1977. Breeding bird survey counts as related to habitat and date. Wilson Bull. 89:543-561.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, & D. Bystrak. 1981. Effects of forest fragmentation on avifauna on the eastern deciduous forest. Pgs 125-205 in Forest island dynamics in man-dominated landscapes. (R. L. Burgess, & D. M. Sharp, eds.) Springer-Verlag, New York.

Wiens, J. A. 1977. On competition and variable environments. Amer. Sci. 65:590-597.

-----. 1981. Single-sample surveys of communities: are the revealed patterns real? Am. Nat. 117:90-98.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Willson, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Zimmerman, J. L. 1985. The birds of Konza Prairie Research Natural Area, Kansas. Prairie Nat. 117:185-192.

TABLE 1-Species for which territories were mapped in the attenuated riparian forest on the tallgrass prairie.

species	# of territories	abbreviation
Northern cardinal	26	CAR
Black-capped chickadee	18	BCC
Great-crested flycatcher	11	GCF
Eastern wood peewee	11	EWP
Field sparrow	9	FSP
Tufted titmouse	8	TTM
House wren	8	HWN
White-breasted nuthatch	7	WBN
Brown thrasher	5	BTH
Northern oriole	5	NOR
Rufous-sided towhee	5	RST
Indigo bunting	4	IBT
Eastern bluebird	3	EBB
Rose-breasted grosbeak	3	RBG
Common yellowthroat	3	CYT
Blue grosbeak	2	BGB
Scarlet tanager	2	SCT
Bewick's wren	2	BWN
Blue-gray gnatcatcher	2	BGG
Bell's vireo	1	BVO
Summer tanager	1	SUT
Louisiana waterthrush	1	LWT

TABLE 2-Habitat variables measured for all territories.

variable	abbreviation	significance level^
Tree canopy width	TC	++
% tree canopy	TRTC	+++
Brush canopy width	BC	+++
% brush canopy	BTOT	+++
Open canopy width	OC	NSD
% open canopy	OTOT	+
Total canopy width	TOTC	++
Forb ground cover	LFC	NSD
Grass ground cover	LGC	+++
Shrub ground cover	LSC	NSD
Shrub cover	LSHB	++
Canopy cover	LCAN	+++
Litter depth	LITD	+++
Canopy height	CANHT	+++
Dead stems, <2.5cm	D1	NSD
Dead stems, 2.5<X<10cm	D2	NSD
Dead stems, 10<X<30cm	D3	+
Dead stems, >30cm	D4	NSD
Live stems, <2.5cm	L1	+
Live stems, 2.5<X<10cm	L2	++
Live stems, 10<X<30cm	L3	NSD
Live stems, >30cm	L4	++

^Significance level of the test for differences between species: +-P= .05, ++-P= .01, +++-P= .0001.

TABLE 3-Amount of variance explained by the principal components.

PC	% variance	cumulative
PRIN1	40	40
PRIN2	19	59
PRIN3	8	67
PRIN4	7	74
PRIN5	6	80

TABLE 4-PC1 loading factors for habitat variables and correlations between PC1 scores and the habitat variables.

habitat variable	loading factor	correlation^
TC	.35	.86+
TRTC	.37	.92+
BC	-.25	-.63+
BTOT	-.33	-.79+
OTOT	-.24	-.59+
TOTC	.29	.72+
LGC	-.15	-.37+
LSHB	.04	-.10
LCAN	.34	.84+
LITD	.26	.63+
CANHT	.36	.89+
D3	-.01	-.02
L1	-.11	-.26+
L2	-.03	-.07
L4	.24	.59+

^Pearson product moment correlations.
+Significant at a=.05.

TABLE 5-PC2 loading factors for habitat variables and correlations between PC2 scores and the habitat variables.

habitat variable	loading factor	correlation^
TC	.02	.04
TRTC	-.01	-.01
BC	.24	.41+
BTOT	.32	.32+
OTOT	-.23	-.39+
TOTC	.04	.07
LGC	-.42	-.72+
LSHB	.50	.84+
LCAN	-.03	-.06
LITD	.20	.35+
CANHT	-.03	-.06
D3	.24	.41+
L1	.43	.72+
L2	.36	.61+
L4	-.04	-.08

^Pearson product moment correlations.
+Significant at a=.05.

TABLE 6-Comparison of types of avian species in the woody riparian vegetation on Konza Prairie, Kansas, to the eastern deciduous forest, Maryland.

species group	Maryland^	Kansas*
Forest interior		
permanent resident	3	2 (2)#
short-distance migrant	1	0 (0)
neotropical migrant	15	6 (3)
subtotal	/19	/8
Forest interior & forest edge		
permanent resident	6	7 (5)
short-distance migrant	10	5 (5)
neotropical migrant	10	7 (5)
subtotal	/26	/19
Forest edge & scrub		
permanent resident	6	5 (4)
short-distance migrant	13	11 (9)
neotropical migrant	9	6 (5)
subtotal	/28	/22
TOTAL	73	49

^information from Whitcomb et al. 1981.
*information from Zimmerman 1985.
#numbers in parenthesis are the number of species that are found in both areas.

TABLE 7-Summary+ of various niche aspects for eleven common species in the woody riparian areas on the tallgrass prairie.

species	diet*	nesting	foraging
CAR	seeds fruit insects	in shrubs	ground
BCC	caterpillars arachnids larvae	SCN^	subcanopy
GCF	lepidopterans coleopterans hymenopterans	SCN	flycatcher
HWN	hemipterans orthopterans lepidopterans	SCN	ground & foliage
TTM	caterpillars hymenopterans coleopterans	SCN	canopy
EWP	dipterans hymenopterans coleopterans	open	flycatcher
WBN	coleopterans arachnids caterpillars	SCN	bark
NOR	caterpillars larvae slow insects	hanging	canopy
FSP	grass seeds weed seeds insects	in grass	ground
RST	coleopterans lepidopterans fruit & seeds	in shrubs	litter
BTH	coleopterans caterpillars hemipterans	in shrubs	ground

+ references are cited in the text.
* top three items in diet in order of importance.
^ SCN=secondary cavity nester.

Figure 1-Mean species response for PC1 and PC2.

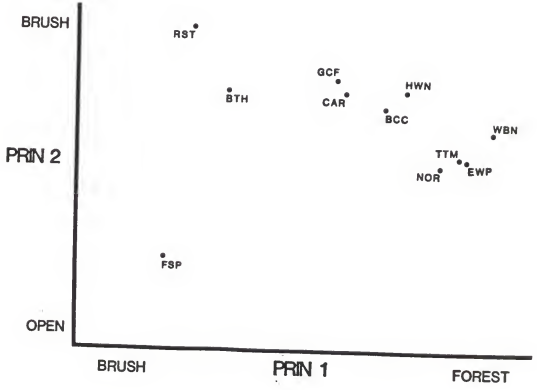


Figure 2-Confidence ellipses for the mean species response along the PC1 and PC2 axes, using all data points.

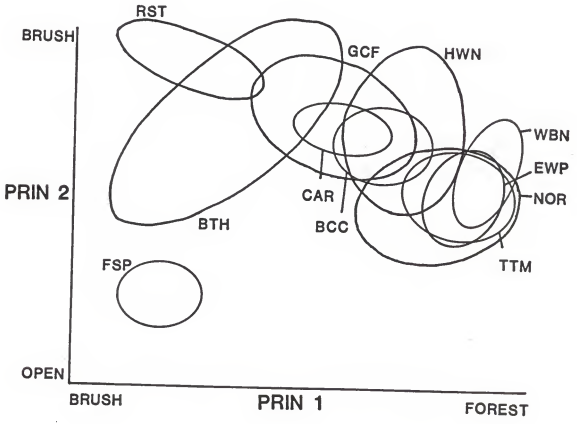


Figure 3-Conficence ellipses for the mean species response for the PC1 and PC2 axes for the forest group, n=5.

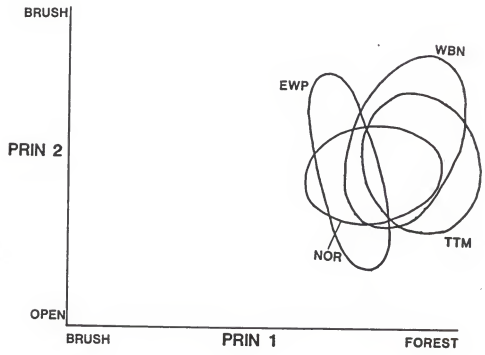


Figure 4-Conficence ellipses for the mean species response for the PC1 and PC2 axes for the brush group, n=5.

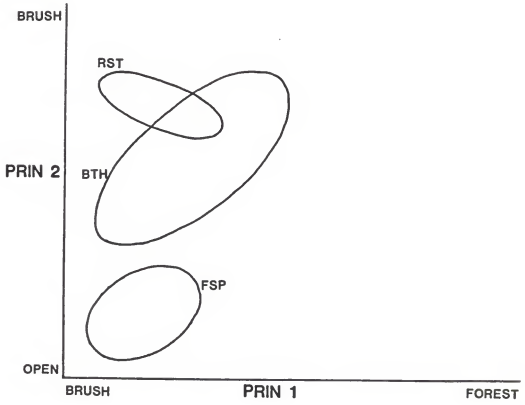


Figure 5-Confidence ellipses for the mean species response for the PC1 and PC2 axes for the generalist group, n=5.

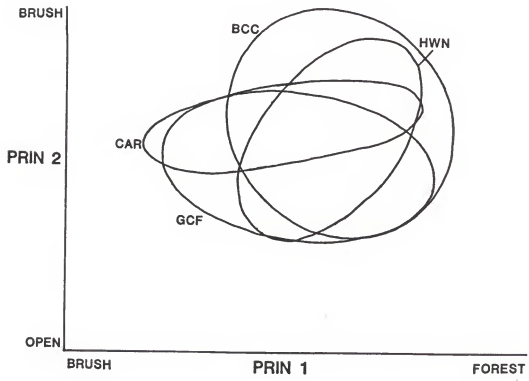
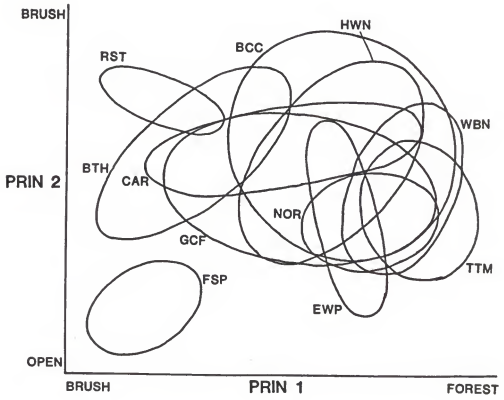


Figure 6-Confidence ellipses for the mean species response along the PC1 and PC2 axes for all species, n=5.



APPENDIX 1-Scientific names for species mentioned in the text.

species	scientific name
Yellow-billed cuckoo	Coccyzus americanus
Common flicker	Colaptes auratus
Red-bellied woodpecker	Melanerpes carolinus
Red-headed woodpecker	Melanerpes erythrocephalus
Hairy woodpecker	Picoides villosus
Downy woodpecker	Picoides pubescens
Great crested flycatcher	Myiarchus crinitus
Eastern wood-pewee	Contopus virens
Blue jay	Cyanocitta cristata
Black-capped chickadee	Parus atricapillus
Tufted titmouse	Parus bicolor
White-breasted nuthatch	Sitta carolinensis
House wren	Troglodytes aedon
Bewick's wren	Thryomanes bewickii
Brown thrasher	Toxostoma tufum
American robin	Turdus migratorius
Veery	Catharus fuscescens
Eastern bluebird	Sialia sialis
Blue-grey gnatcatcher	Polioptila caerulea
Yellow-throated vireo	Vireo flavifrons
Black-and-white warbler	Mniotilta varia
Northern parula	Parula americana
Ovenbird	Seiurus aurocapillus
Louisiana waterthrush	Seiurus motacilla
Common yellowthroat	Geothlypis thrichas
Kentucky warbler	Oporornis formosus
Hooded warbler	Wilsonia citrina
Common grackle	Quiscalus quiscula
Northern oriole	Icterus galbula
Scarlet tanager	Piranga olivacea
Summer tanager	Piranga rubra
Northern cardinal	Cardinalis cardinalis
Rose-breasted grosbeak	Pheucticus ludovicianus
Blue grosbeak	Guiraca cairulea
Indigo bunting	Passerina cyanea
American goldfinch	Carduelis tristis
Rufous-sided towhee	Pipilo erythrophthalmus
Field sparrow	Spizella pusilla

APPENDIX 2-Mean species response@ for habitat variables.

species	TC *	TRTC #	BC *	BTOT #	OC *	OTOT #	TOTC *	LFC ^	LGC ^	LSC ^	LSHB ^
CAR	**73.1**	**.64**	**16.2**	**.21**	**13.2**	**.15**	**102**	**.18**	**.27**	**.36**	**.47**
	62.9	.26	12.8	.20	12.4	.16	57.8	.16	.19	.30	.22
BCC	**91.0**	**.71**	**11.6**	**.15**	**14.2**	**.14**	**116**	**.21**	**.25**	**.32**	**.43**
	67.6	.22	9.1	..14	15.8	.17	61	.15	.23	.21	.22
GCF	**64.4**	**.69**	**18.9**	**.26**	**10.4**	**.15**	**89.7**	**.22**	**.12**	**.33**	**.45**
	63.4	.29	17.8	.23	10.7	.16	60.4	.17	.13	.22	.20
TTM	**82.8**	**.85**	**3.0**	**.05**	**8.6**	**.01**	**94.4**	**.16**	**.31**	**.27**	**.30**
	53.7	.10	2.7	.05	8.6	.10	51.2	.10	.25	.22	.06
EWP	**110**	**.81**	**9.2**	**.07**	**12.7**	**.12**	**132**	**.23**	**.32**	**.24**	**.27**
	46.6	.14	13.5	.12	11.8	.12	38.7	.13	.20	.13	.22
WBN	**137**	**.87**	**7.42**	**.05**	**9.6**	**.07**	**154**	**.23**	**.17**	**.36**	**.30**
	49.6	.10	4.8	.03	7.2	.07	44.3	.16	.17	.18	.27
FSP	**27.1**	**.34**	**20.0**	**.32**	**20.6**	**.34**	**67.7**	**.09**	**.69**	**.20**	**.15**
	25.4	.24	13.1	.21	9.4	.17	32.8	.08	.23	.18	.17
HWN	**63.5**	**.74**	**11.1**	**.13**	**11.2**	**.13**	**85.9**	**.10**	**.24**	**.41**	**.41**
	36.1	.22	10.3	.10	13.9	.13	35.2	.06	.22	.22	.31
BTH	**35.0**	**.40**	**30.2**	**.42**	**15.2**	**.19**	**80.4**	**.17**	**.34**	**.31**	**.49**
	26.5	.21	7.8	.16	7.4	.09	30.5	.10	.22	.16	.22
NOR	**103**	**.91**	**2.2**	**.03**	**4.8**	**.06**	**110**	**.35**	**.30**	**.20**	**.26**
	53.5	.09	3.5	.04	5.8	.08	47.9	.51	.21	.14	.15
RST	**16.4**	**.38**	**29.6**	**.51**	**8.6**	**.12**	**54.6**	**.22**	**.22**	**.46**	**.54**
	5.5	.23	18.5	.17	8.7	.09	29.8	.14	.11	.35	.14

@ mean response is in boldface, standard deviation below.
* units are meters.
percentage of total canopy width.
^ arcsine transformation of percent cover values.

APPENDIX 2 continued-Mean species@ response for habitat variables

species	LCAN ^	LITD $	CANHT *	D1 +	D2 +	D3 +	D4 +	L1 +	L2 +	L3 +	L4 +
CAR	**.66**	**1.8**	**7.7**	**37.8**	**2.5**	**.31**	**.15**	**70.8**	**11.7**	**2.2**	**.57**
	.36	.61	5.1	38.9	3.0	.68	.46	55.1	10.8	2.3	.86
BCC	**.73**	**1.8**	**8.7**	**31.8**	**2.2**	**.28**	**0.0**	**62.3**	**10.4**	**2.4**	**.83**
	.27	.42	4.4	25.2	2.5	.57	0.0	58.9	8.7	2.7	1.4
GCF	**.58**	**2.1**	**8.4**	**23.6**	**1.2**	**.45**	**.27**	**92.3**	**5.7**	**.91**	**.82**
	.28	.40	6.1	22.5	5.6	1.2	.47	1.0	6.0	1.6	.87
TTM	**.88**	**2.3**	**12.8**	**20.4**	**2.4**	**.50**	**.25**	**33.2**	**5.2**	**2.4**	**1.9**
	.20	.54	3.8	25.7	2.6	.92	.46	29.2	8.7	2.0	1.1
EWP	**.88**	**2.2**	**13.6**	**14.5**	**.54**	**.18**	**0.0**	**40.4**	**4.4**	**2.3**	**1.6**
	.23	.47	2.3	15.4	1.0	.40	0.0	52.2	6.2	2.3	.92
WBN	**.99**	**2.0**	**13.3**	**8.7**	**1.0**	**.57**	**.28**	**46.6**	**2.0**	**2.7**	**1.0**
	.16	.67	2.6	10.9	1.2	.98	.49	54.4	2.1	2.8	1.2
FSP	**.09**	**.74**	**.83**	**17.3**	**.33**	**0.0**	**0.0**	**25.4**	**1.0**	**.78**	**0.0**
	.12	.39	.54	18.8	.71	0.0	0.0	34.5	2.3	1.3	0.0
HWN	**.79**	**2.5**	**10.9**	**24.0**	**2.1**	**1.5**	**.38**	**71.6**	**4.5**	**1.2**	**1.2**
	.28	.63	3.6	10.0	2.5	1.5	.74	76.8	4.8	1.6	1.2
BTH	**.46**	**1.6**	**3.3**	**33.6**	**2.0**	**0.0**	**.20**	**75.8**	**9.8**	**1.0**	**.40**
	.42	.62	1.8	17.8	2.7	0.0	.45	88.4	7.8	1.2	.55
NOR	**.67**	**1.8**	**10.8**	**21.2**	**2.2**	**.20**	**0.0**	**42.8**	**6.4**	**2.4**	**1.0**
	.29	.57	3.7	18.1	2.5	.45	0.0	58.0	6.6	3.3	.71
RST	**.29**	**1.3**	**3.9**	**50.6**	**3.2**	**.60**	**.20**	**163**	**11.0**	**1.8**	**.40**
	.19	.23	2.1	37.6	3.7	1.3	.45	52.8	4.8	2.5	.89

@ mean response is in boldface, standard deviation below.
^ arcsine transformation of percent cover values.
$ units are centimeters.
* units are meters.
+ (number X 100) = # woody stems/ha.

APPENDIX 3-Summer resident^ birds in the woody riparian vegetation on the tallgrass prairie.

Forest interior

PR*	SD*	Neotropical migrants
Hairy woodpecker		Louisiana waterthrush
White-breasted nuthatch		Kentucky warbler
		Scarlet tanager
		Summer tanager
		Rose-breasted grosbeak
		Chuck will's widow

Forest interior and forest edge

Red-bellied woodpecker		Yellow-billed cuckoo
	Northern flicker	
Downy woodpecker		Black-billed cuckoo
	Eastern phoebe	
Blue jay		Great crested flycatcher
	Gray catbird	
Tufted titmouse		Eastern wood-pewee
	Common yellowthroat	
Northern cardinal		Blue-gray gnatcatcher
	Rufous-sided towhee	
Black-capped chickadee		Red-eyed vireo
Red-headed woodpecker		Warbling vireo

Forest edge and scrub

Northern bobwhite		Eastern kingbird
	Mourning dove	
American crow		Orchard oriole
	House wren	
European starling		Northern oriole
	Brown thrasher	
Northern mockingbird		Blue grosbeak
	American robin	
Loggerhead shrike		Indigo bunting
	Eastern bluebird	Bell's vireo
	Common grackle	
	Brown-headed cowbird	
	American golfinch	
	Field sparrow	
	Bewick's wren	
	Lark sparrow	

^ Species list from Zimmerman (1985).
* PR=permanent resident, SD=short-distance migrant.

AVIAN HABITAT SELECTION IN THE ATTENUATED RIPARIAN FOREST ON THE TALLGRASS PRAIRIE

by

FRED L. MIKESELL

B.S., Kansas State University, 1984, 1985

AN ABSTRACT OF A THESIS

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requirements for the degree

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BIOLOGY

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ABSTRACT

Woody vegetation extends out onto the prairie in narrow projections, grading from forested areas at the lower reaches of the streams to a brushy thicket in the upper reaches of the streams. Avian habitat selection was studied to ascertain what habitat variables determine where birds are found along this gradient. At randomly selected sites, territories were mapped for eleven common species, and various habitat variables measured within each territory. Principal components analysis was performed on the data. The two principal components, which explained 59% of the total variation, are the brush-tree axis (40% of the variation) and the open-brushy axis (19%). Species were separated into three groups on the basis of these axes. Forest birds, which included the tufted titmouse, eastern wood-pewee, white-breasted nuthatch, and northern oriole, were only found in the forested regions. Brush birds, which included the field sparrow, brown thrasher, and rufous sided towhee, were found only in the thickets at the upper reaches of the streams. Generalists, including the northern cardinal, black-capped chickadee, great crested flycatcher, and house wren, were found throughout the forest-brush gradient. There is considerable overlap in the type of habitat selected within each group but only minimal amounts between groups. Species within each group are separated by differences in other aspects of their niche, such as diet, foraging, and reproductive behavior.